

KOLOPSIS YPERUS SP. NOV. (ZYGOMATURINAE, MARSUPIALIA)
FROM THE ONGEVA LOCAL FAUNA: NEW EVIDENCE FOR
THE AGE OF THE ALCOOTA FOSSIL BEDS OF CENTRAL AUSTRALIA.

PETER MURRAY¹, DIRK MEGIRIAN² AND RODERICK WELLS³

¹ Northern Territory Museum,

P.O. Box 2109, Alice Springs, NT 0871, Australia.

² Northern Territory Museum,

P.O. Box 4646, Darwin, NT 0801, Australia.

³ Flinders University, School of Biological Sciences,

G.P.O. Box 2100, Adelaide, SA 5001, Australia.

ABSTRACT

The Ongeva Local Fauna from central Australia, which yielded a zygomaturine upper third premolar, upper second molar and upper first incisor, is situated unconformably above the lacustrine sediments containing the Alcoota Local Fauna. The teeth, representing *Kolopsis yperus* sp. nov. are intermediate in size and morphology to the Alcoota LF *K. torus* Woodburne, 1967, and *Zygomaturus gilli*, Stirton, 1967, from the Beaumaris Local Fauna, Victoria. The new species is interpreted to be advanced over *K. torus*, though less derived than *Z. gilli* from Beaumaris. The occurrence of an undetermined *Kolopsis* species at Beaumaris, Victoria, has led to the suggestion that the Alcoota and Beaumaris Local Faunas are both of similar (probably early Pliocene) age, though other evidence points to an earlier age for the Alcoota Local Fauna. Recovery of a derived *Kolopsis* species from a stratum of the Waite Formation in unconformable superposition to the Alcoota Local Fauna supports a pre-Beaumaris age, possibly late Mitchellian Stage equivalency, of the Alcoota Local Fauna.

KEYWORDS: *Kolopsis yperus* sp.nov., new species, Ongeva Local Fauna, Alcoota Local Fauna, Waite Formation, Miocene, central Australia, biochronology, biostratigraphy.

INTRODUCTION

Woodburne (1967:160) described fragmentary vertebrate remains from Hill 1, Alcoota Station (UCMP Locality V6347), central Australia, as "a meagre concentration of bone much higher in the fluviatile beds...", concluding that "The origin of the fossils from this locality was probably quite different from that of the other quarries, and it is possible that a different depositional environment is indicated".

Hill 1, or Red Hill, is a 20 m high erosional remnant of the Waite Formation, located about 400 m southeast of the main Alcoota vertebrate quarries (Woodburne 1967), (Fig. 1). Dispersed, undiagnostic crocodile, dromornithid bird and diprotodontid marsupial bone fragments have been collected from the surface of this site each

field season by palaeontologists from the Northern Territory Museum. In 1991, surface erosion from recent rainfall exposed a concentration of material that indicated which of the beds were most likely to contain *in situ* fossil bone. Excavation of the apparent source revealed the presence of relatively abundant, though fragmented and chemically weathered, fossil material within a fluviatile horizon. Among the first fossils recovered were an upper third premolar and an associated upper second molar of *Kolopsis yperus* sp. nov., a form with a dentition similar to, but larger than that of the zygomaturine diprotodontid *Kolopsis torus* Woodburne, 1967. The find is significant because it supports the interpolative dating of the biostratigraphically unique and unconformably lower Alcoota Local Fauna to within the late Miocene.

Prior to the recovery of specifically assignable elements characterizing a new local fauna *sensu* Tedford (1970) designated here as the Ongeva Local Fauna, the age of the Alcoota Local Fauna was poorly constrained by the stage of evolution of its diprotodontid species. Diprotodontids of the Alcoota Local Fauna are more derived than the Northern Territory Bullock Creek species but less so than closely related taxa from Beaumaris, Victoria. In the absence of intervening biochrons, local or regional stratigraphic correlates or radiometric age estimates, the Alcoota Local Fauna had been considered to lie at some undetermined point between the late Miocene and early Pliocene (Woodburne 1967, Woodburne *et al.* 1985).

Stirton *et al.*'s (1967) estimated late Miocene age of the Alcoota Local Fauna appeared to be supported by the presence in the Beaumaris Local Fauna of a primitive *Zygomaturus* species, *Z. gilli* Stirton, 1967. The Beaumaris marsupials are derived from the marine Sandringham Sands Formation and are assigned to the Cheltenhamian Stage on the basis of marine megafossils. A Beaumaris zygomaturine dentary was described by Woodburne (1969) as belonging to the same species, but a second specimen of *Z. gilli*, a lower molar collected in 1972, indicated that Woodburne's specimen is not *Z. gilli*, but apparently represents a species of *Kolopsis* (Rich 1976). Based on the assumption that the Beaumaris *Kolopsis* might indicate a stage-of-evolution equivalent to *K. torus*, the upper age limit of the Alcoota Local Fauna was taken to be contemporaneous with Beaumaris or possibly

even later (Woodburne *et al.* 1985). However, Woodburne *et al.* (1985) also observed that the phyletic ties of the Alcoota Fauna are apparently much closer to the mid Miocene faunas than to any of the undoubted lower Pliocene assemblages.

This paper presents some new stratigraphic and palaeontological evidence that argues for a pre-Beaumaris age for the Alcoota Local Fauna. Many of the concepts currently in use in Australian mammal biochronology were introduced by R.A. Stirton and co-workers. The biochronologic framework presented by Stirton, Woodburne and Plane (1967: Fig. 2), based on what has become known as the 'stage-of-evolution' method, has proved remarkably robust in its basic form, though subsequent discoveries have led to refinements and elaboration (e.g. Woodburne *et al.* 1985).

The phylogeny of the Zygomaturinae remains the best resolved of the biochronologically useful mammal lineages. Within the Zygomaturinae, the genera *Neohelos* Stirton, *Kolopsis* Woodburne and *Zygomaturus* Owen could be viewed as chronogenera. In broad Lyellian terms, *Neohelos* is viewed as an index genus for the early and mid Miocene, *Kolopsis* characterises the late Miocene, and *Zygomaturus* is essentially Pliocene and Pleistocene. Some species of these genera can provide even finer biochronological resolution, as elaborated on below.

Prefixes to catalogue numbers are as follows: NMV, Museum of Victoria (National Museum of Victoria), Melbourne; SGM, Spencer and Gillen Museum (Museums and Art Galleries of the Northern Territory) Alice Springs; UCMP,

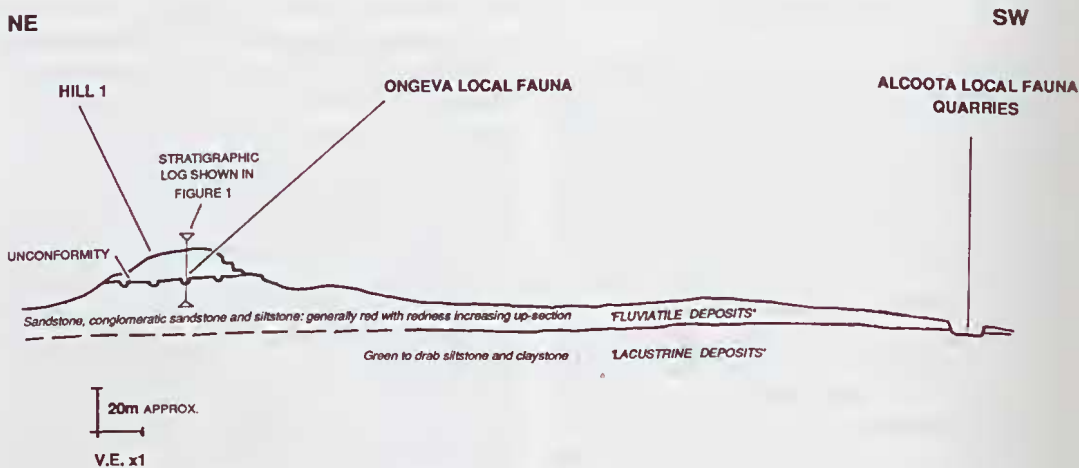


Fig. 1. Cross section through Waite Formation sediments showing the interpreted stratigraphic relationship between Ongeva and Alcoota Local Faunas. Apart from the recognition of an unconformity in the sequence, the stratigraphy follows Woodburne (1967: Fig. 2).

University of California Museum of Paleontology, Berkeley.

ANATOMICAL ABBREVIATIONS

BM	Buccal margin of P ³ crown
CIA	Central incisor alveolus of premaxilla
DIE	Digastric eminence of dentary
DIS	Postdigastric sulcus of dentary
ENG	Enamel cap of I ¹
IIF	Interincisive fossa of premaxilla
INF	Incisive foramen of premaxilla
MAC	Submasseteric crest of dentary
MAF	Masseteric fossa of dentary
MEC	Metacone
MEF	Mental foramen of dentary
MFO	Masseteric foramen of dentary
ML	Midline of premolar and molar crowns
PAC	Paracone
PAS	Parastyle
P-M	Para-metaconal crest of P ³
PMS	Premaxillo-maxillary suture
PRC	Protocone
SPM	Septal process premaxilla

STRATIGRAPHY

Ongeva Locality. A comprehensive account of the geology of the Waite Formation is provided by Woodburne (1967). Attention is focussed here on aspects relevant to the Ongeva Local Fauna. The new fauna was recovered from Waite Formation sediments cropping out on the northwestern face of Hill 1 (Fig. 1) at or very close to the University of California Museum of Paleontology vertebrate fossil locality V6347, known as the "Red Hill Locality" (Woodburne 1967:162). A vertical stratigraphic section through the fossil quarry is shown in Figure 2 and is comparable to Woodburne's (1967:175) Section 1, measured nearby on the southwestern side of the mesa. As detailed below, the new fauna occurs stratigraphically above an unconformity, represented by an ancient weathered surface and profile inferred to have formed upon and within the sedimentary sequence containing the Alcoota Local Fauna (Fig. 1).

Woodburne (1967) recorded Hill 1 vertebrate fossils as occurring in a "light buff, pebble conglomerate" that crops out as a resistant ledge. He interpreted the ferruginous pebbles as reworked nodules from the laterite profile that

forms part of the basement to the Waite Formation. However, these ferruginous pebbles or pisolites are matrix-supported and show reverse grading within the unit. In thin-section they do not resemble the lateritic pisolites developed on the basement complex at Hills 5 and 6, though little significance can be attached to this observation as nothing is known of the regional petrologic variability of basement lateritic pisolites. Primary sedimentary structures (bedding, scouring, sorting, normal grading, channel lags) are absent at the Hill 1 occurrence, and, as revealed by quarrying, the pisolitic bed is succeeded by an unlithified accumulation of pisolites that had evidently weathered out of their matrix and remained as an erosional lag.

In thin-section the pisolites incorporate silt to coarse sand-sized, very angular to sub-rounded quartz (including polycrystalline grains), minor feldspar and lithic grains, cemented by iron oxides (probably goethite and haematite). The siliceous material comprises up to 50% of the pisolites. The different grains are present in the same proportions with shapes and size ranges the same as in the intervening matrix of pale green, sandy silt. The siliceous grains incorporated in the pisolites appear to have been concentrated by the removal, and/or alteration (primarily oxidation with volume reduction) of the fine fraction of the matrix. Most of the ferruginous clasts are spherical, but some are irregularly shaped with sharp projections and seem unlikely to have survived transportation in that form. No abraded quartz grains are present at the pisolite surfaces. Some pisolites show a very weak, coarse concentric lamination. Others are only weakly indurated by iron oxides and are interpreted as representing incipient stages of development. The rock is veined and cemented by a diagenetic, sparry calcite cement, some of which fills circumgranular fractures around the pisolites.

A transported origin for the Hill 1 occurrence of pisolites is incompatible with the features described above. The evidence points to their *in situ* genesis within a weathering profile, with concentration of weathered-out pisolites developed as a lag at the former land surface, a common succession in pisolitic laterite profiles (c.g. McFarlane 1983: Fig. 2.19). The ancient weathered surface represents an unconformity within the Waite Formation separating the stratigraphically lower lacustrine sediments hosting the Alcoota Local Fauna from later sediments containing the Ongeva Local Fauna.

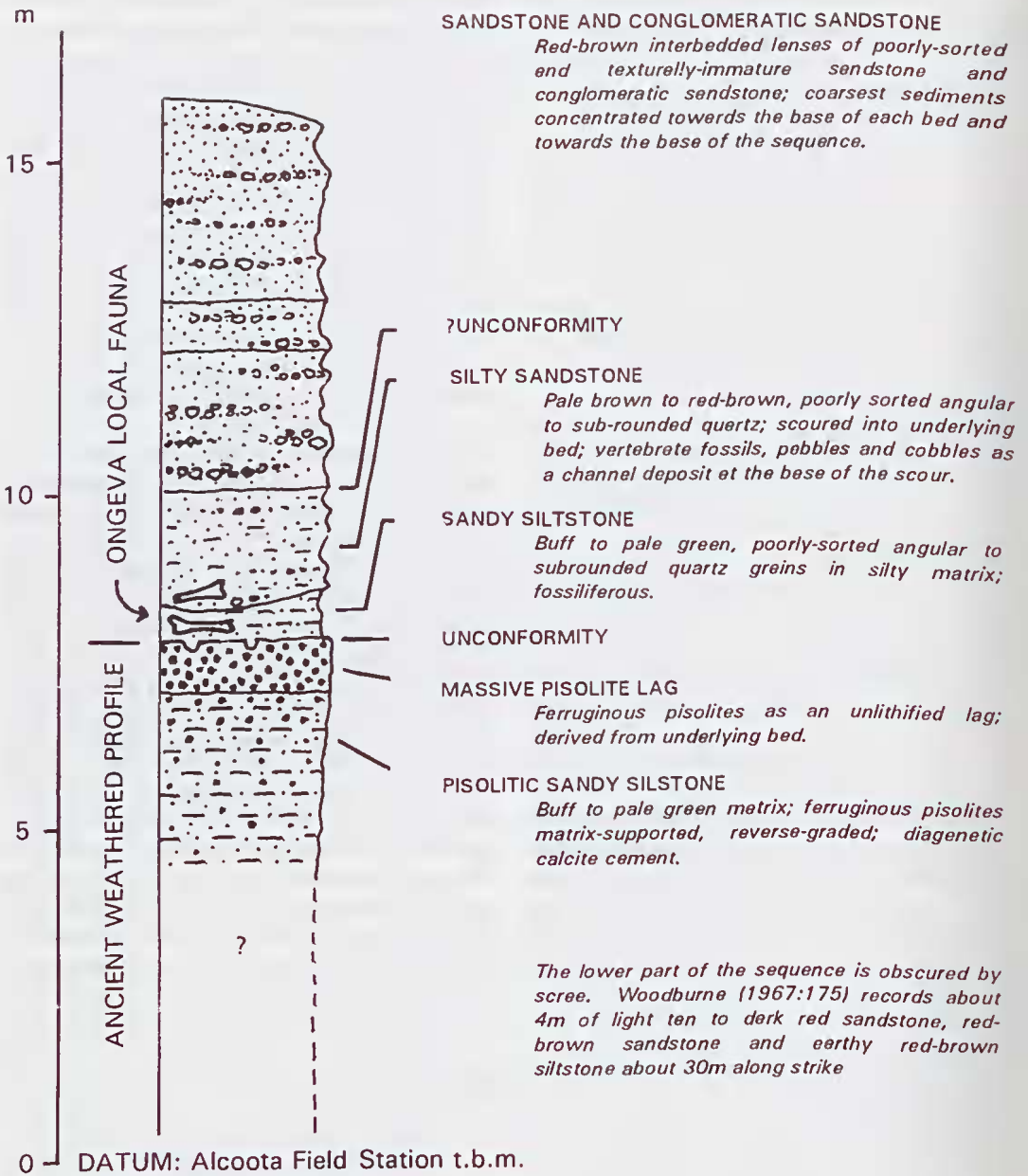


Fig. 2. Stratigraphic section through the *Kolopsis yperus* sp. nov. type locality.

The Ongeva Local Fauna fossils are hosted in two distinct beds. The lower bed consists of a buff to pale green, sandy silt, while the upper consists of pale brown silty sandstone. The contact between the two is irregular and, where it can be traced from the quarry along strike to a point about 10 m to the west, has a relief of about 0.8 m. The coarser upper bed appears to have been scoured into the sandy silt with fossils concentrated at the base of the scour, along with a few

isolated cobbles. The scour is thought to represent a local feature in an otherwise conformable sequence: there is no evidence to suggest that the two fossiliferous beds are separated by a significant depositional hiatus.

Woodburne (1967:187) recorded chalcidonic limestone caprocks at two topographic levels near the New Well Site, approximately 15 km west of Hill 1. He considered them to be in stratigraphic succession and suggested that Ter-

tiary fossils of varying ages might be present in the Waite Basin, a conclusion supported by the new discoveries reported here. The recognition of an unconformity within the Waite Formation does not require amendment of lithostratigraphic nomenclature (Staines 1985).

PALAEONTOLOGY

Ongeva Local Fauna. Surface fossils consist of fragments of dromornithid lower limb bones, isolated crocodile teeth, crocodile osteoderms and indeterminate fragments of mammalian bone. An edentulous fragment of an immature diprotodontid dentary (cf. *Kolopsis* sp.) was recovered in 1990.

In the lower unconsolidated silty bed, partially intact dromornithid bird, crocodile, macropodid and diprotodontid remains including the zygomatic upper teeth described below, were confined to a thin horizon about 200 mm above the unconformity. The large dromornithid long bones show depositional orientation with their long axes bearing 355° to 50°. The surfaces of the bones are etched by numerous fine rootlets and possibly by endogenous chemical weathering due to soil development near the surface. The bone is mineralized and less fragile than the "lacustrine bed" material of the Alcoota Local Fauna.

Several large dromornithid elements and a series of diprotodontid vertebrae, recovered from the overlying sandy bed, are also assigned to the Ongeva Local Fauna, although no biochronologically useful material was recovered from this horizon. A rind of coarse, sandy matrix is cemented to these bones by sparry calcite cement.

Determinations of the fauna from the silty and sandy beds of the Ongeva faunal unit are as follows: Crocodylidae - cf. *Quiukaua* Molnar; Dromornithidae - cf. *Dromornis stirtoni* Rich; Macropodidae - cf. *Dorcopsoides fossilis* Woodburne; Diprotodontidae - undetermined Zygomaticurinae, cf. *Kolopsis* Woodburne; Zygomaticurinae - *Kolopsis yperus* sp. nov. Of these, the macropodid and the zygomaticurine diprotodontid are of biochronological interest. The macropodid is represented by a metatarsal IV and some phalanges. We have not attempted to determine a species from the macropodid postcranial elements in anticipation of teeth being found later.

SYSTEMATICS

Family Diprotodontidae Gill
Subfamily Zygomaticurinae
Stirton, Woodburne and Plane
Genus *Kolopsis* Woodburne

Type species: *Kolopsis torus* Woodburne, 1967, by original designation and monotypy.

Kolopsis yperus sp. nov.
(Figs 3-9; Tables 1, 2)

Type material. Holotype: SGM P92117 right P³ and right M².

Referred specimens. SGM P92115 edentulous right premaxilla fragment with incisor alveoli and premaxillomaxillary suture; SGM P92114 right I¹; SGM P92119 right dentary fragment with P₃ alveolus, part of the lower incisor alveolus and mental foramen; SGM P92116, left dentary fragment preserving masseteric fossa and foramen, digastric sulcus and anterior margin of pterygoid fossa.

Type locality. Alcoota Station, Northern Territory, latitude 22°52'S, longitude 134°27'E. The holotype was recovered from an unlithified sandy silt of the Waite Formation, about 200 mm above an unconformity on the north side of Hill 1, 9.8 m higher than the fossiliferous lacustrine sediments containing the Alcoota Local Fauna, about 2 km southwest of the junction of Ongeva and Waite Creeks.

Fauna. Ongeva Local Fauna (new).

Rock unit and age. Waite Formation, Cheltenhamian Stage equivalent, late Miocene-early Pliocene.

Diagnosis. Distinguished from *Zygomaturus gilli* Stirton, 1967, in being smaller, with more elongated and transversely narrower P³ crown; deeper, wider cleft separating the parastyle from the paracone on P³; paracone and metacone of P³ situated closer together; and long postmetacrista. Distinguished from all other *Zygomaturus* species in possessing large parastyle and metastyle on M²; more elongate, transversely narrower M²; straight, nearly vertical premaxillary suture commencing from significant distance behind I³ as opposed to posteriorly arcuate suture commencing from immediately behind I³. Distinguished from *Kolopsis rotundus* Plane, 1967, in being larger; P³ of *K. rotundus* otherwise differs from *K. yperus* in the same respects as given for *Zygomaturus* (Murray, 1992). Dentary differs

from that of *Kolopsis* sp. from Beaumaris (Woodburne 1969) in being larger, in having postdigastric sulcus deeper and masseteric foramen well-developed. Compares and contrasts with *K. torus* Woodburne, 1967, in the following respects: all elements larger and more robust than *K. torus*; P³ crown ovate and relatively elongated, similar to *K. torus* but slightly longer; P³ parastyle base and cingulum expanded lingually but protocone less prominent lingually than in *Kolopsis torus*. Paracone and metacone situated close together and postmetacrista long; metacone situated anterior to level of hypocone as in *K. torus*; posterolabial cingulum ascends postmetacrista and defines broad shallow posterolabial fossa behind metacone as in *K. torus*. Crest between paracone and protocone low, comparable to *K. torus* specimens in which it is present; para-metaconal shearing crest higher and slightly less lingually inclined than in *K. torus*. M² larger in proportion to P³; M² more elongated and rectangular as opposed to trapezoidal in outline in *Kolopsis torus*, but less square and relatively narrower than in *Zygomaturus*

species. M² parastyle and metastyle massive as in *Kolopsis torus*. Interloph valley relatively wide as in *Kolopsis torus* but with slightly less curvature of the protoloph. Posterolingual cingulum and base of the hypocone more expanded than in *K. torus*. I¹ large in proportion to I²⁻³ alveoli as in *Zygomaturus* spp., but with compressed crown and root and flattened mesial surface similar to *Kolopsis torus*. Premaxillo-maxillary suture commences laterally a considerable distance posterior to I³ and ascends vertically in straight line to contact nasals, as in *Kolopsis torus*. Dentary postdigastric sulcus and pterygoid fossa confluent as in *Kolopsis torus*.

Etymology. *Υπερ* "υπερ", (Greek) meaning "above".

Description. The type and referred specimens of *K. yperus* were found in very close proximity at the same level and probably belong to one individual. The upper premolar and second molar lay together. On the basis of their corresponding interproximal surfaces, stage of wear, and size, we consider the cheek-teeth to represent an individual.

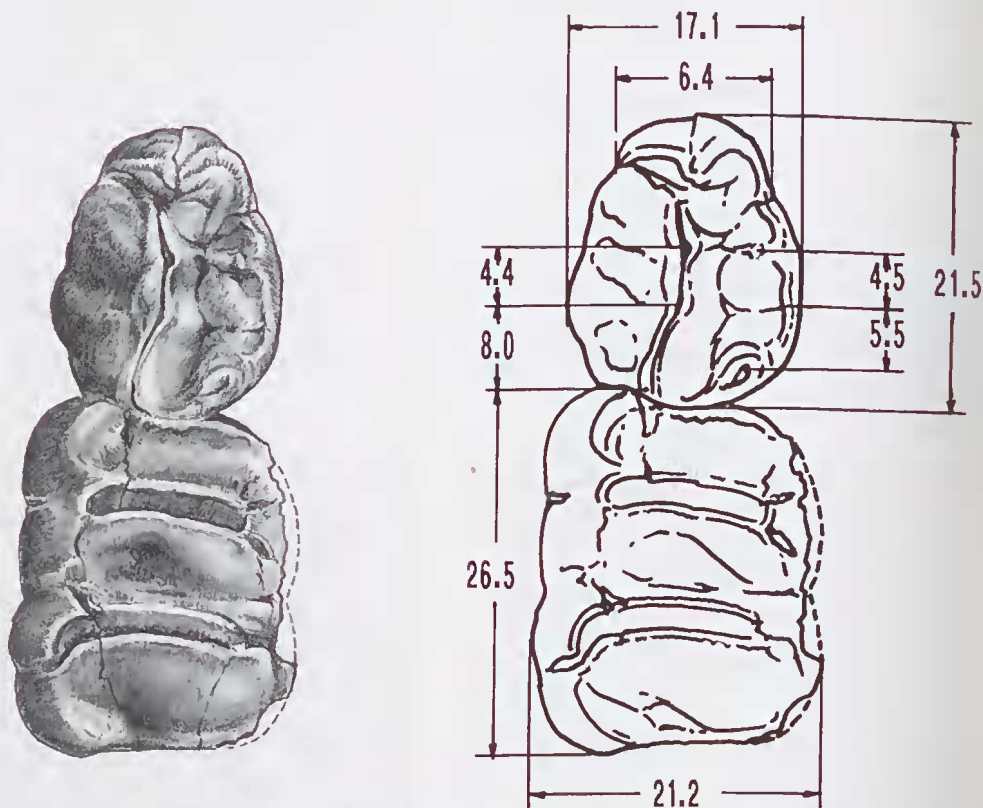


Fig. 3. Ongeva Local Fauna *Kolopsis yperus* sp. nov. Holotype SGM 92117 (upper third premolar and upper second molar) in occlusal view; dimensions in millimetres shown on line drawing.

Upper incisor (Figs 4, 5, 7, 8). The crown is subtriangular in section and is capped by enamel over the anterolateral surface of the tip. The occlusal facet is stepped in lateral profile and elliptical in occlusal view. The lateral surface is convex over the extent of the crown, becoming progressively more compressed over the remaining three-fourths of the tooth. A broad, shallow

indentation of the lateral side of the root is centred at about the mid point of its total length. The medial surface is flat over its entire length. A shallow sulcus and low crest follows the mid-lateral contour of the crown extending over most of the length of the root. The longitudinal axis of the root and crown is straight. The root is open. The maximum depth of the root is 26.0 mm,

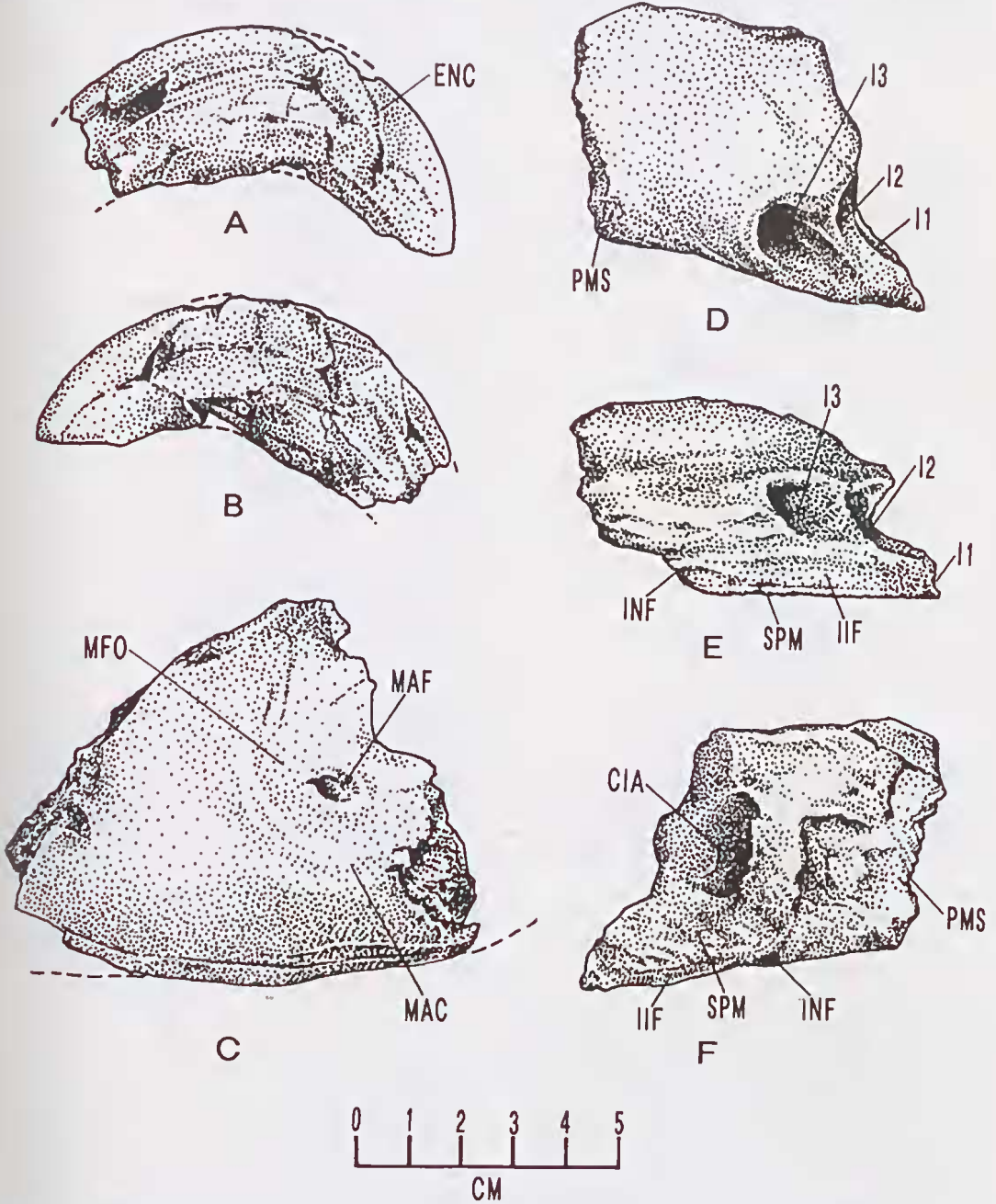


Fig. 4. Referred specimens of *Kolopsis yperus* sp. nov.; A, lateral aspect and B, medial aspect of right upper incisor (SGM P92114); C, left dentary fragment preserving masseteric fossa (SGM P92116); D, lateral, E, ventral and F, medial aspects of right premaxilla fragment preserving I¹⁻³ alveoli, margin of incisive foramen and premaxillo-maxillary suture (SGM P92115).

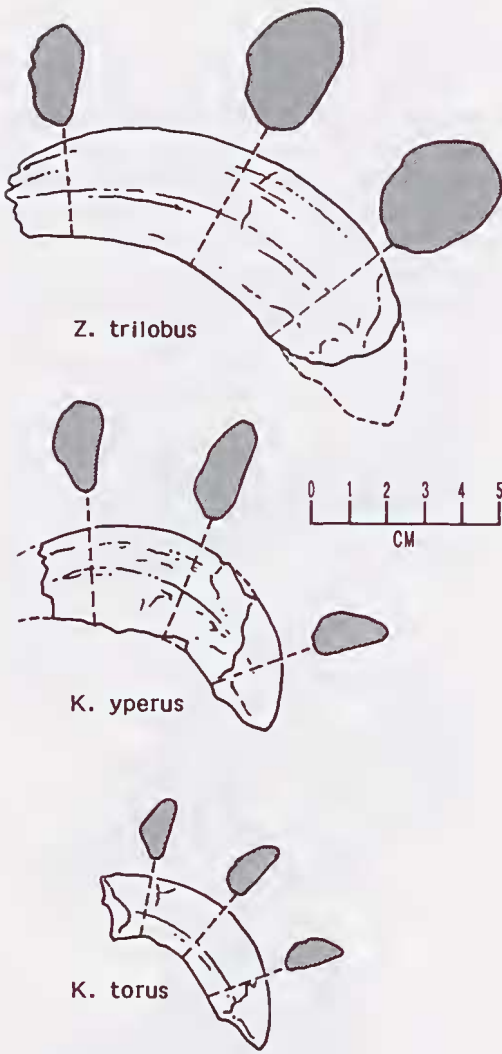


Fig. 5. Comparison of 1st morphology in *Zygomaturus trilobus* Macleay, *Kolopsis yperus* sp. nov. and *Kolopsis torus* Woodburne; note flattened internal surfaces in *Kolopsis* species compared to the more rounded internal surfaces in *Zygomaturus trilobus* (character 13).

thickness 18.2 mm. The length of the dorsal curvature is 105.0 mm.

Upper third premolar (P³) (Figs 3, 6). The upper third premolar is 21.5 mm long and 17.1 mm wide, within a millimetre in each dimension of the largest *Kolopsis torus* specimen in the NTM collection (SGM P1006, 20.6 mm X 16.2 mm) and at least 1.7 mm shorter than *Zygomaturus gilli* in which the anterior portion of the parastyle is abraded. The occlusal outline shape is oval; tapering slightly more anteriorly than posteriorly. The parastyle is transversely broad. The para-metaconal shearing crest lies near the longitudi-

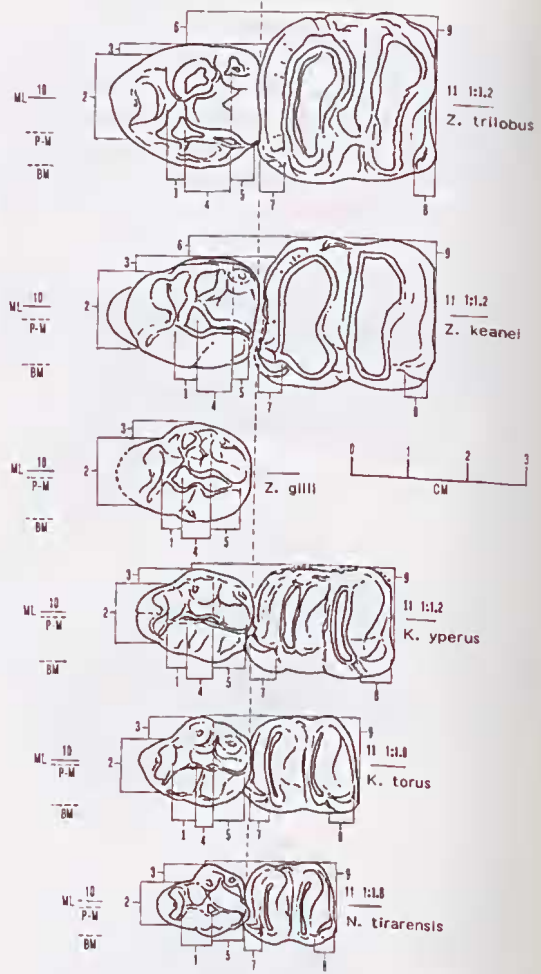


Fig. 6. Diagrammatic representation of character morphocline in P¹-M² of zygomaturines; structurally-primitive species is *Neohelos tirarensis* Stirton. Definition of characters: 1, extent of separation of the parastyle from the paracone; 2, transverse width of the parastyle; 3, extent of lingual protrusion of the protocone relative to the lingual side of the parastyle; 4, extent of separation of the paracone from the metacone; 5, length of the postmetacrista; 6, extent to which the P³ is narrower than the M² on the lingual side; 7, size and development of the parastyle; 8, size and development of the metastyle; 9, extent of posterolingual expansion of the base of the hypocone; 10, lines expressing the distance of the para-metaconal crest (P-M) from the midline of the crown (ML) and from the buccal margin of the crown (BM); 11, ratio of P³ length to M² length.

nal midline of the crown (Fig. 6). The lingual base of the parastyle is expanded by a shelf-like cingulum that extends to the anterolingual base of the protocone. The parastyle leans posteriorly towards the paracone and in terms of relative proportions, these cusps may be just perceptibly closer together than in *K. torus*, though multiple caliper measurements yielded no consistent dif-

ferences. The paracone and metacone are separated by a broad, shallow vertical sulcus on the buccal side of the main shearing crest. The cusps are relatively higher and are connected by a higher crest than in *K. torus*. The paracone and metacone are situated close together, with the metacone and its internal buttress transversely aligned with the sulcus between the protocone and hypocone. The paracone is 4.4 mm from the metacone in *K. yperus*. The P³ postmetaerista in *K. yperus* is 8.0 mm long. A low, V-shaped transverse crest connects the lingual base of the paracone with the labial base of the protocone. The posterolabial base of the protocone contacts the anterolingual side of the internal metaconal buttress enclosing a small depression. The labial egingulum is poorly preserved on the specimen, but appears to have been weak and largely confined to the postparaconal portion of the crown. The posterolabial egingulum merges with the postmetaerista to form a low metastyle. A broad postmetaconal sulcus is present labially.

Upper second molar (M²) (Figs 3, 6). The occlusal outline of the *K. yperus* upper second molar crown is an elongate, rectangular shape. The M² of *K. yperus* is considerably larger than in *Kolopsis torus* and also relatively narrower in proportion to its length. The length of the crown is 26.5 mm and the maximum width is 21.2 mm. Both labial loph phases are elongated due to the large parastyle anteriorly and equally large metastyle posteriorly. The preparaerista and postmetaerista are correspondingly well developed. The protoloph is transversely narrower than the hypoloph and slightly curved. A weak mesostyle is present in the labial end of the interloph sulcus. The interloph sulcus forms an anteriorly slanted V-shaped cleft, wider labially than lingually and proportionally similar to that of *Kolopsis torus*. The protoconal base gently swells posteriorly into the mid-valley to about the same extent as in *K. torus*, thus leaving a considerable gap at the base of the sulcus. The postparaconal and premetaconal buttresses are poorly developed. The lophs are slightly worn but appear to have been relatively lower than in *K. torus*. The anterior egingulum is well developed and shelf-like, merging with the parastyle labially and terminating lingually at the anterior base of the protocone. Labial and lingual egingulae are absent. The posterior egingulum is a low, rounded, sinuous crest originating on the labial base of the hypocone and merging with the metastyle labially. The base of the hypocone is

expanded posterolingually and is both higher and considerably broader than the protocone.

Premaxilla fragment (Figs 4, 7, 8). The premaxilla fragment is referred to *K. yperus* on the basis of its association with the other material, its evident zygomatourine morphology and by the morphology of the central incisor alveolus, which is of the correct size and shape for the associated upper I¹. The fragment represents the right premaxilla, terminating posteriorly at the premaxillo-maxillary suture and broken dorsally

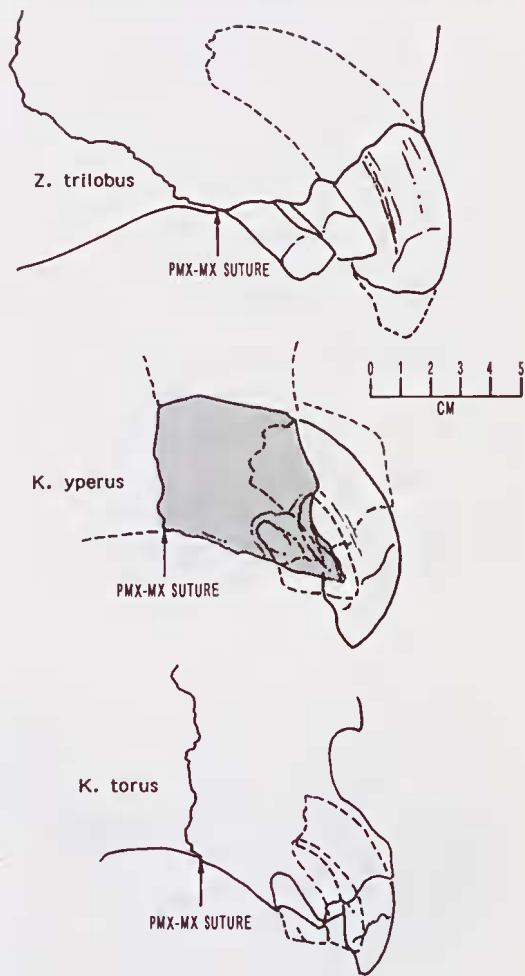


Fig. 7. Comparison of the morphology of the premaxillary fragment of *K. yperus* sp. nov. (stippled) with *Zygomaturus* and *K. torus* Woodburne; *K. yperus* is synplesiomorphically aligned with *K. torus* in having a nearly vertical premaxillo-maxillary suture that commences near the middle of the diastema in contrast to *Zygomaturus trilobus* Macleay in which the suture is arcuate and commences close to I¹ (character 12); the size of the I¹ relative to the other incisors is suggested in the illustration; *K. yperus* central incisors are proportionally enlarged compared to *K. torus*, but less enlarged than in *Zygomaturus trilobus* (character 14).

at an indeterminate distance, perhaps about 30–40 mm, below the nasal contact. All three upper incisor alveoli are present. The fragment shows close similarities to the same region in *Neohelos* and *Kolopsis torus*. The alveolus for I³ is slightly larger in diameter and has a deeper socket than that of I². A sulcus, corresponding to the inferior margin of I¹, is inscribed on the anteromesial edge of the fragment near the midline, indicating that the incisor crowns were closely approximated. The interincisival fossa is shallow and narrow (Fig. 8). The anterior margin of the incisive foramen is located 40.0 mm behind the posterior margin of the I¹ alveolus. The septal process is short transversely. The premaxillo-maxillary suture commences its near-vertical ascent to the nasals approximately 28.0 mm behind the posterior alveolar margin of I³ (Fig. 7). The base of the lateral margin of the nasal cavity (Fig. 4F) is represented on the fragment indicating that *K. yperus* had a large, broad, tubular external narial aperture.

Dentary (Figs 4, 9). The dentary is represented by a fragment of a left posterior portion of the horizontal ramus and a fragment of a right anterior portion of the horizontal ramus which includes the P₃ alveolus and upper half of the mental foramen (Figs 4C, 9). Except for their larger proportions and stronger expression of muscular attachments, the specimens are the basic shape of a *Kolopsis torus* dentary (Fig. 9).

The submasseteric crest is pronounced and the masseteric fossa is relatively deep, but somewhat confined in extent. A large masseteric foramen is present. The posterior margin of the digastric eminence is just evident. The inferior border is thick and strongly inflected resulting in a pronounced postdigastric sulcus. The postdigastric sulcus is apparently confluent with the anterior portion of the pterygoid fossa. The inferior margin of the fragment shows a shallow concavity at the transition from the digastric eminence to the angular process.

Comparative remarks. The fossils assigned to *K. yperus* are significantly larger and more robust than comparable *Kolopsis torus* and *Kolopsis rotundus* material. *Kolopsis yperus* is also considerably larger than the *Beaumaris Kolopsis* sp. assigned to *Z. gilli* by Woodburne (1969) but reassigned to *Kolopsis* by Rieh (1976) (Figs 6, 9). *Kolopsis yperus* is somewhat smaller than *Zygomaturus gilli* and much smaller than *Zygomaturus keanei* Sürton and *Zygomaturus trilobus* Mæleay.

The right I¹ of *K. yperus* closely resembles that of *K. torus*, differing primarily in being much larger and relatively deeper in proportion to its transverse thickness (Fig. 5). As in *K. torus* and in contrast to *K. rotundus* and *Zygomaturus trilobus*, the mesial (internal) surface of the I¹ is perfectly flat as opposed to convex. The longitudinal axis of the crown and root is straight.

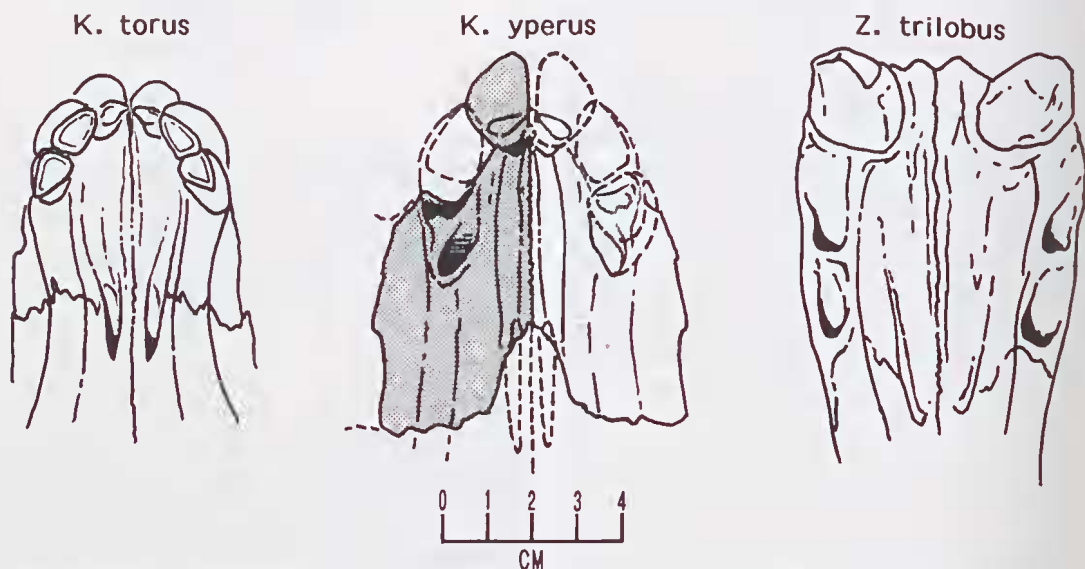


Fig. 8. Comparison of the morphology of the premaxillary palate of *K. yperus* sp. nov. (restored) with *K. torus* Woodburne and *Zygomaturus trilobus* Mæleay; The interincisive fossa of *K. yperus* is narrower and shallower than in *K. torus* and *Z. trilobus*, but otherwise more closely resembles *K. torus* in the shape of the incisor arcade and position of the I³ alveolus relative to the premaxillo-maxillary suture and position of the incisive foramina.

Kolopsis yperus also shares with *K. torus* a broad, shallow indentation of the lateral side of the incisor, which appears to correspond to the marial margin of the premaxilla in the latter

species. Because of the detailed similarities of the central incisor and its relations with the referred premaxilla to the corresponding structures in *K. torus*, it can be inferred that the upper

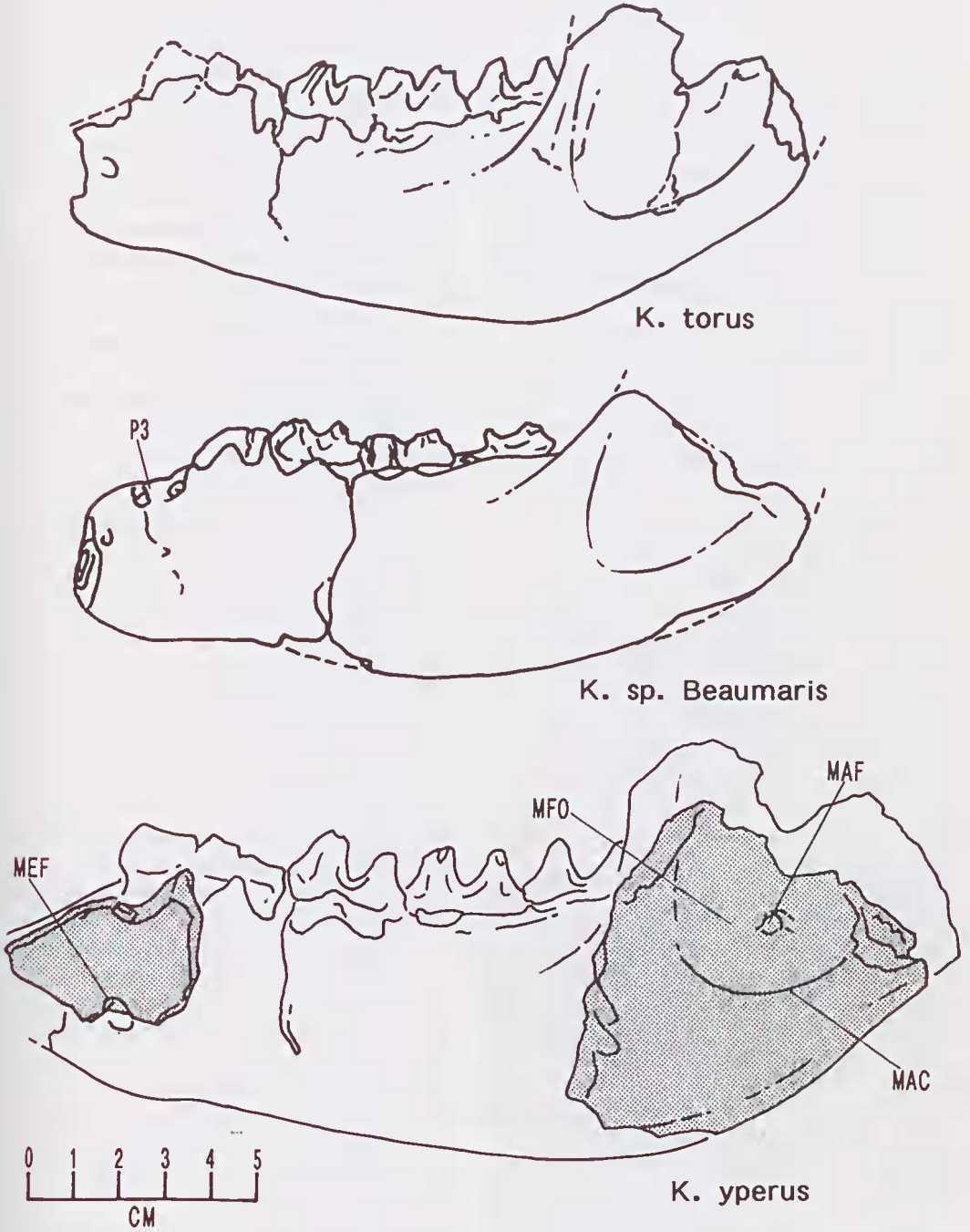


Fig. 9. Comparison of the size and morphology of dentary fragments of *K. yperus* sp. nov. (restored) with outlines of *K. torus* Woodburne (SGM P87132) and *K. sp.* from Beaumaris, (NMV P15911A and P1591) (Woodburne 1969). The hypothetical outline of *K. yperus* is derived from an enlarged *K. torus* dentary (SGM P8664); note that *K. yperus* is considerably larger and more robust than other *Kolopsis* species; the mental foramen (MEF) may have been situated relatively low as in *Zygomaturus trilobus* Macleay; a large masseteric foramen is present in *K. yperus* (MAF). The masseteric foramen is usually absent or very small in *K. torus*, and is absent in the Beaumaris *Kolopsis* sp.

incisor crown tips of *K. yperus* were convergent. In *Zygomaturus trilobus* the incisor crowns are divergent and the longitudinal axis of the crown and root is bowed. In *K. rotundus*, the axis of the crown and root is also distinctly curved so as to project the tip of the crown lateral to the midline of the root (Plane 1967:112, Fig. 2b).

The P³ of *K. yperus* is structurally intermediate between that of *Zygomaturus gilli* and *K. torus*. The P³ morphology of *K. yperus* does not closely resemble that of *K. rotundus*, in which the gap between the parastyle and paracone is greatly reduced, the paracone and metacone are widely separated, the postmetaerista is short, and in which the axis of the para-metaconal crest is situated further from the midline of the crown. The P³ morphology of *K. rotundus* differs from that of *K. yperus* with respect to the same characters as the P³s of *Zygomaturus trilobus*, *Z. keanei* and to a lesser extent, *Z. gilli*. The P³ of *K. yperus* more closely resembles those of both *Z. gilli* and *K. torus* than the P³ of *K. rotundus*. Except for its much smaller size, the spatial relationships of the cusps P³ of *K. rotundus* bear a stronger resemblance to the P³ of *Z. keanei* than to those of other *Kolopsis* species.

The P³ morphology of *K. yperus* is similar to that of *K. torus* in having a wide gap between the parastyle and the paracone, the paracone and metacone situated close together (e.g. in *K. torus*, the paracone is 3.5-4.0 mm from the metacone; in *K. yperus* the paracone is separated from the metacone by 4.4 mm; in the smaller *K. rotundus*, the paracone is separated from the metacone by at least 5.0 mm), and in having a long postmetaerista, which in *Zygomaturus* species and *K. rotundus* is very short.

The P³ of *K. yperus* shows an evolutionary trend towards *Zygomaturus* species in that the buccal margin of the para-metaconal crest is less inclined towards the midline of the crown than in *K. torus*; the base of the parastyle is much wider than in *K. torus* resulting in a reduction of the apparently more prominent lingual projection of the protocone; the paracone and metacone are transversely broader and slightly more separated than in *K. torus* and the P³ is shorter relative to the length of the M² than in *K. torus*, the ratio being the same (1:1.2) as in *Zygomaturus keanei* and *Zygomaturus trilobus*, compared to a 1:1.0 ratio in *K. torus* and *Neohelos tirarensis* Stirton (Fig. 6).

The M² of *K. yperus* closely resembles that of *K. torus* in possessing a large parastyle and a

large metastyle. In *Zygomaturus* species the M² parastyle and metastyle are reduced. The M² of *K. yperus* differs from *K. torus*, being more elongated and in having a posterolingually expanded base of the hypcone, which results in a more rectangular shape of the occlusal outline of the crown. In *K. torus* the occlusal outline of the crown is distinctly trapezoidal (Fig. 6). The crown proportions of *K. yperus* differ from *Zygomaturus* species in being narrower relative to their width, in having a less well developed postparaconal buttress, in having a wider interloph sulcus and in that the posterior loph faces are more strongly slanted anteriorly. Although the M² of *K. rotundus* is not known, the M³ protoloph is broad and the crown is squarish, suggesting that its M² was also relatively broad for its length. As in *Zygomaturus* species, *K. rotundus* possesses stronger postparaconal-premetaconal buttresses on M³⁻⁴ than does *K. torus* and inferentially stronger buttresses than *K. yperus* in which the M² postparaconal buttresses are only slightly more conspicuous than in the latter species.

The morphology of the premaxilla fragment of *K. yperus* indicates that it had relatively large central incisors, though not as large in proportion to the I²⁻³ in *Zygomaturus trilobus* (Figs 7, 8). The basic shape of the premaxillary fragment resembles that of *K. torus* in that the incisor arcade is more C-shaped as opposed to the U-shaped arcade in *Z. trilobus*. The interincisive fossa of *K. yperus* appears to have been relatively narrower and shallower than in either *K. torus* or *Zygomaturus trilobus*.

The lateral surfaces of the premaxillary fragment are more deeply concave than in *K. torus*, indicating that the alveolar process was narrower in proportion to the base of the nasal aperture. However, the fragment preserves sufficient points to indicate that the nasal aperture was situated low and that the lateral premaxillary margins did not retreat posteriorly to the extent seen in *Z. trilobus*, in which the lateral margins of the nasal aperture are deeply notched and the base of the aperture is preched high above the premaxillary palate. The I² alveolus of *K. yperus* is distinctly shorter and slightly smaller in diameter than the I³ alveolus. In *Neohelos tirarensis*, the I² alveolus is larger and deeper than the I³ alveolus. In *K. torus* the I² and I³ alveoli are approximately the same size. In *Z. trilobus* the I² alveolus is slightly smaller than the I³ as in *K. yperus*. However, in *Z. trilobus*, both I² and I³ are greatly reduced in size relative to I¹.

The dentary fragments of *K. yperus* provide the only points of comparison with the *Kolopsis* sp. specimen from Beaumaris (Fig. 9). The lower jaw of *K. yperus* was considerably larger and more robustly proportioned than that of the Beaumaris species, and slightly larger, though considerably more robust, than any specimen of *K. torus* from Alcoota. The submasseteric crest is more prominent and the masseteric fossa is relatively deeper, though somewhat more confined in anteroposterior extent than either *K. torus* or the Beaumaris *Kolopsis*. Unlike *K. torus* or *K. sp.* from Beaumaris, *K. yperus* possesses a large masseteric foramen. The internal side of the dentary differs from that of the Beaumaris species in having a deep postdigastric sulcus and a strongly inflected crest of the inferior border. Several specimens of *K. torus* from the Alcoota Local Fauna approach this degree of inflection of the inferior border and corresponding depth of the postdigastric sulcus, but none is as robustly constructed as *K. yperus*. The proportions and shape of the dentary of the Beaumaris *Kolopsis* are not substantially different from the more typical and rather variable *Kolopsis torus* material from Alcoota.

The deep postdigastric sulcus of *K. yperus* is therefore more comparable to the condition in *Zygomaturus keanei* than to that of the Beaumaris *Kolopsis* sp. (Stirton 1967). However, *K. yperus* resembles *Kolopsis torus* in having a confluent postdigastric sulcus and pterygoid fossa. In *Zygomaturus* species the anterior margin of the pterygoid fossa is elevated above the digastric fossa and the fossae are divided by a low crest. In *K. yperus*, the fragment extends posteriorly far enough to have retained evidence of the feature, if such a division was present. Although only the posterior margin of the digastric eminence is preserved on the *K. yperus* specimen, the probable extent and shape of the structure is apparent. The projected outline of the inferior border indicates that the digastric eminence was in about the same position and similar in shape and proportion to that of *K. torus*. In particular, the concavity between the digastric eminence and the inferior border below the pterygoid fossa is poorly developed. In *Zygomaturus* species the digastric eminence is more posteriorly situated, deeper and more prominently offset by a distinct concavity behind.

The fragment of right dentary preserves a 2.3 mm length of the lower incisor alveolus, the P₃ alveolus and the superior margin of the symphy-

sis. Alignment of the fragment with the symphyseal region of a *K. torus* dentary shows that the lower incisor of *K. yperus* was significantly less procumbent than in the majority of *K. torus* specimens (Fig. 9). Because this feature is vari-

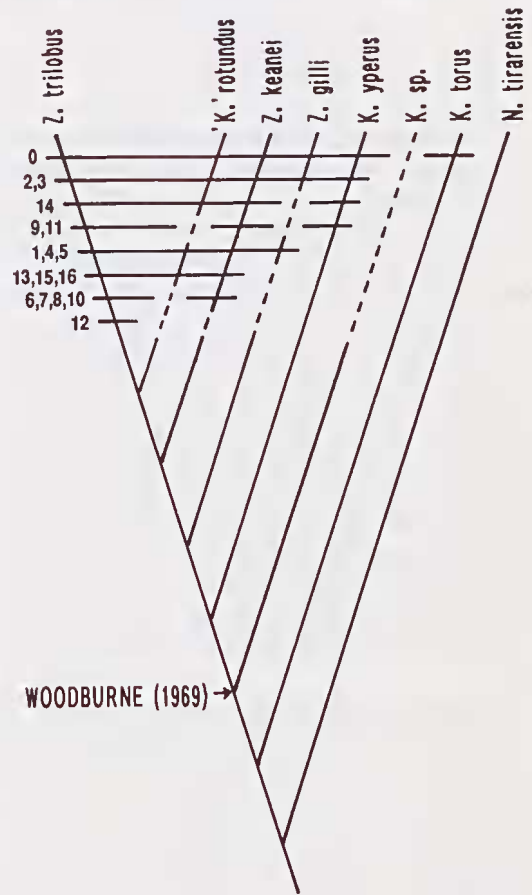


Fig. 10. Dendrogram showing the relative stage-of-evolution of *K. yperus* to *Zygomaturus* and *Kolopsis* species. Numerical designations of characters are defined in Table 1. Because the genus *Zygomaturus* is based on more than one character state, the assessment of the clade is equivocal. *Kolopsis yperus* is assigned to the genus *Kolopsis* on the basis of its symplesiomorphic resemblances to *K. torus*, and lack of derived features characteristic of *Zygomaturus*. On the basis of the material available for comparison, *K. yperus* is structurally intermediate between *Z. gilli* and *K. torus*. There are no diagnostic points of comparison between *K. yperus* and *K. sp.* from Beaumaris (Woodburne 1969). The Beaumaris specimen is situated between *K. torus* and *K. yperus* because Woodburne (1969:38) considered *K. sp.* to be advanced over *K. torus* in having "...more strongly developed and curved metalophid and asymmetrically V-shaped transverse valleys of the molars, and the flattened essentially open posterior root of the lower incisor." On the basis of the character definition and morphocline used here, "*K.*" *rotundus* is more closely aligned with species of the genus *Zygomaturus* than with species of the genus *Kolopsis*.

able in *K. torus*, the condition is significant to the extent that the estimated state of lower incisor recumbency in *K. yperus* is rarely found in *K. torus*, being more characteristic of *Zygomaturus* species.

DISCUSSION

A primary purpose of this paper is to provide an assessment of the stage-of-evolution of the Ongeva Local Fauna zygomaturine, and thereby better constrain the chronostratigraphy of the Waite Formation. Character states by which the stage-of-evolution (plesiomorphic or apomorphic) of selected zygomaturine species can be compared (Table 1) are presented as a matrix in Table 2. The structurally-primitive state in Zygomaturinae is exemplified by *Neohelos* species. The contents of the character state matrix are depicted as a dendrogram in Figure 10. This dendrogram should be viewed as an indicator of the stage-of-evolution of selected taxa, rather than as a phylogenetic hypothesis. Were the species included in the cladogram contemporaneous, it might be reasonable to interpret such a dendrogram as a phyletic tree. However, the production of a dendrogram from

a character state matrix can force the use of branchings that are simply not tenable as hypotheses of evolution. As outlined in the introduction, at the generic level, *Neohelos*, *Kolopsis* and *Zygomaturus* are essentially in ancestor-descendent relationships. Figure 10 is a diagram that indicates only the pattern of character distributions (Nelson and Platnick 1974; Maddison *et al.* 1985:85).

The recognition of ancestor-descendent lineages (or indeed 'interealary' lineages, *sensu* Stirton *et al.* 1967) has implications for the formal aspects of taxonomy, as already pointed out by Stirton *et al.* (1967:152) for the dipronditid sub-families investigated by them:

"As in the diagnoses of other taxonomic groups, not all the characters listed completely separate every genus within a subfamily from all other members of the family (Dipronditidae). Each subfamily lineage extends across a wide span of time and contains different genera. Therefore, each point given in a subfamily diagnosis may not apply equally to all members of the lineage."

For the purposes of taxonomy, we have defined the genus *Kolopsis*, in part, on the basis of the lack of the derived states which define *Zygomaturus*. In an essentially anagenetic se-

Table 1. *Neohelos tirarensis* represents the plesiomorphic species within the Subfamily Zygomaturinae by which the stage-of-evolution of species of *Kolopsis* and *Zygomaturus* are gauged. Abbreviations and definitions: 0=plesiomorphic undivided state of the para-metacone of P³; 1=extent of separation of the P³ parastyle from the paracone; 2=transverse width of the base of the parastyle of the P³; 3=extent of the development of a concave profile between the lingual side of the parastyle and the anterior base of the protocone; 4=relative extent of separation of the paracone and metacone of the P³; 5=relative length of the postmetacrista of the P³; 6=transverse width of the P³ in comparison to the width of M²; 7=relative size of the parastyle of M²; 8=relative size of the metastyle of M²; 9=relative expansion of the hypocone base of M²; 10=relationship of the para-metaconal crest to the midline of the P³ crown (ML=midline; BM=huccal margin); 11=ratio of the length of the P³ to the length of M²; 12=morphology of the premaxillomaxillary suture; 13=shape and orientation of the first upper incisor crowns; 14=size of the upper first incisors relative to the size of I² and I³; 15=relations of the postdigastric sulcus and pterygoid fossa (RAMAL FOSSAE); 16=relative extent of development of the digastric eminence (DIE) and the postdigastric sulcus (DIS).

CHARACTER	PLESIOMORPHIC STATE	APOMORPHIC STATE
0 para-metacone	undivided	divided
1 cleft, PAS-PAC	narrow	wide
2 width parastyle	narrow	wide
3 PRC-PAS concavity	deep	shallow
4 PAC-MEC distance	close together	far apart
5 postmetacrista	long	short
6 M ² -P ³ width	P ³ equal	P ³ narrower
7 M ² parastyle	large	small
8 M ² metastyle	large	small
9 M ² hypocone base	narrow	broad
10 P-M to midline	close to ML	close to BM
11 P ³ :M ²	1:1.0	1:1.2
12 PMX-MX suture	vertical, mid-diastemal	arcuate, near I ³
13 I ¹ crown	flat mesial, convergent	round, divergent
14 I ¹ size	small	large
15 ramal fossae	confluent	separate
16 DIE and DIS	weak, shallow	strong, deep

quence, the nomenclatural transition from one genus to another is arbitrary, but can still be rigorously defined, satisfying the requirements of formal taxonomy, even though *Kolopsis* cannot be defined by synapomorphies.

The assignment of the new species to the genus *Kolopsis* is based primarily upon its symplesiomorphic resemblances to *K. torus*: closely situated paracone and metacone of P³; straight, vertical premaxillomaxillary suture commencing well behind I¹; compressed, mesially flat, convergent I¹; retention of large parastyle and metastyle on M²; relatively open midvalley of M²; weak digastric eminence; confluent postdigastric sulcus and pterygoid fossa (Fig. 10, Tables 1, 2).

The more closely approximated paracone and metacone and elongated postmetacrista of the P³ is the primary indication of the slightly more primitive state of *K. yperus* relative to *Zygomaturus gilli*. The species is otherwise apomorphically aligned with *Zygomaturus* in the following respects: I¹ are large relative to other upper incisors; the parastyle of P³ is transversely broad and the M² is rectangular due to expansion of the hypocone base.

Kolopsis yperus shows no closer resemblances to the late Pliocene Awe Local Fauna

zygomaturine *Kolopsis rotundus* than it does to *Zygomaturus* species. *Kolopsis rotundus* shares numerous derived features with *Zygomaturus* species including a more oval cross section and curvature of the longitudinal axis of I¹; P³ paracone and metacone widely separated and situated closer to the buccal side of the crown; short parametacrista; parastyle closely approximated to the paracone. Its appearance much higher in the stratigraphic column and its close resemblance to *Zygomaturus* spp. indicate that *K. rotundus* is either convergent with *Zygomaturus* or that it should be included within the genus *Zygomaturus* as a new combination.

Ambiguity in the assignment of these zygomaturines is largely due to their fragmentary condition and a lack of comparable structures. *Zygomaturus gilli* lacks an M² for comparison with *K. yperus* and other species of *Zygomaturus*. The Beaumaris *Kolopsis* sp. is represented only by lower dentition precluding a direct comparison with *K. yperus*. Because the transition to *Zygomaturus* appears to be a mosaic structural succession, involving many features of the skull and dentition, the present information cannot provide documentation of a detailed phylogenetic sequence from *Kolopsis* to *Zygomaturus*. However, the forms under exami-

Table 2. Distribution of character states among zygomaturine genera; numbers correspond to definitions in Table 1 and Figure 6.

	<i>Zygomaturus trilobus</i>	<i>Kolopsis rotundus</i>	<i>Zygomaturus keanei</i>	<i>Zygomaturus gilli</i>	<i>Kolopsis yperus</i>	<i>Kolopsis</i> sp. from Beaumaris	<i>Kolopsis torus</i>	<i>Neohelos tirarensis</i>
0	A	A	A	A	A	-	A	P
1	A	A	A	A	P	-	P	P
2	A	A	A	A	A	-	P	P
3	A	A	A	A	A	-	P	P
4	A	A	A	A	P	-	P	P
5	A	A	A	A	P	-	P	P
6	A	-	A	-	P	-	P	P
7	A	-	A	-	P	-	P	P
8	A	-	A	-	P	-	P	P
9	A	-	A	-	A	-	P	P
10	A	-	A	-	P	-	P	P
11	A	-	A	-	A	-	P	P
12	A	-	-	-	P	-	P	P
13	A	A	A	-	P	-	P	P
14	A	A	A	-	A	-	P	P
15	A	A	A	-	P	P	P	P
16	A	A	A	-	P	P	P	P

nation are sufficiently close to one another structurally to indicate that the transition to *Zygomaturus* was finely incremental.

In describing the *Zygomaturus gilli* dentition, Stirton (1967:134) remarked that "Because they appear to be intermediate between *Kolopsis* and *Zygomaturus* their generic assignment might be questionable...". In the example of *Kolopsis yperus*, we have a species that appears to represent an intervening structural condition that could have given rise to *Zygomaturus gilli*. The evidence supports Stirton *et al.* (1967) in their view that a member of the genus *Kolopsis* gave rise to *Zygomaturus* through a gradualistic structural sequence. In terms of stage-of-evolution chronology, *Kolopsis yperus* suggests that the Ongeva Local Fauna is slightly older than the Beaumaris Local Fauna.

Compared to *K. torus*, the unnamed Beaumaris *Kolopsis* species also appears to be a derived form possessing some *Zygomaturus*-like characters. Woodburne (1969:38) considered the following features to be sufficient to assign the specimen to *Zygomaturus*: elongate proportions of the molars, well-developed arcuate metalophid and laterally compressed but open proximal cross section of the lower incisor. Comparison of the fragmentary remains of *K. yperus* with the Beaumaris *Kolopsis* provides an indication that they are distinct, though perhaps equally derived species.

SUMMARY AND CONCLUSIONS

Ongeva Local Fauna and Beaumaris Local Fauna diprotodontids are at a more similar stage-of-evolution than the Alcoota and Beaumaris representatives are to each other. Because the Ongeva faunal unit is considerably higher in the stratigraphic column and unconformably separated from the Alcoota Local Fauna, it follows that the Alcoota Local Fauna is considerably older than the Beaumaris Local Fauna, as the structural and systematic affinities of its diprotodontid fauna have consistently indicated (Woodburne *et al.* 1985).

The Beaumaris Local Fauna is a well-dated vertebrate fauna by virtue of the associated marine megafossils within the Black Rock Member of the Sandringham Sands Formation. The relative age of the Alcoota Local Fauna from central Australia may now be constrained more confidently on the basis of the relative stage of evolution of the Ongeva Local Fauna

zygomaturine *K. yperus*. If *Z. gilli* (Beaumaris Local Fauna) and *K. yperus* (Ongeva Local Fauna) represent the Cheltenhamian Stage, then perhaps *K. torus* (Alcoota Local Fauna) represents the later part of the Mitchellian Stage.

ACKNOWLEDGEMENTS

Credit for the discovery of mammal teeth on Hill 1 belongs to Fraser McGregor and Lisa Correl who took on the challenge of excavating the site in the final days of our 1991 stay at Alcoota. We acknowledge the sterling efforts of the other members of the Flinders University party as well as our volunteers, and extend thanks to Tom and Wendy Webb for their hospitality at Alcoota. Thomas Rich and Michael Plane read and commented on a draft of the manuscript, which has been improved by their efforts. We also appreciate the editorial assistance of Helen Larson and Alice Wells of the Northern Territory Museum. Palaeontological work at Alcoota was undertaken with the assistance of a National Estate Program Grant (Northern Territory).

REFERENCES

- Maddison, W.P., Donaghue, M.J. and Maddison, D.R. 1984. Outgroup analysis and parsimony. *Systematic Zoology* **33**(1):83-103.
- McFarlane, M.J. 1983. Laterites. In: Goudie, A.S. and Pye, K. (eds) *Chemical sediments and geomorphology*, pp. 7-58. Academic Press, London.
- Murray, P. 1992. Smallest New Guinea zygomaturines - derived dwarfs or relict plesiomorphs? *The Beagle, Records of the Northern Territory Museum of Arts and Sciences*, **9**(1):89-110.
- Nelson, G. and Platnick, 1981. *Systematics and biogeography: cladistics and vicariance*. Columbia University Press, New York.
- Plane, M.D. 1967. Two new diprotodontids from the Pliocene Otibanda Formation, New Guinea. In: *Tertiary Diprotodontidae from Australia and New Guinea*. Bureau of Mineral Resources, Geology and Geophysics, Australia, Bulletin **85**:105-128.
- Rich, T.H. 1976. Recent fossil discoveries in Victoria. Five Late Cenozoic fossil Marsupial sites in Victoria: a progress report. *The Victorian Naturalist* **93**(5): 198-206.
- Staines, H.R.E. 1985. Field geologists guide to lithostratigraphic nomenclature in Australia. *Australian Journal of Earth Sciences* **32**:83-106.
- Stirton, R.A. 1967. New species of *Zygomaturus* and additional observations on *Meniscolophus*. Pliocene Palankarinna Fauna, South Australia.

- In: *Tertiary Diprotodontidae from Australia and New Guinea*. Bureau of Mineral Resources, Geology and Geophysics, Australia, Bulletin 85:129-150.
- Stirton, R.A., Woodburne, M.O. and Plane, M.D. 1967. A phylogeny of the Tertiary Diprotodontidae and its significance in correlation. In: *Tertiary Diprotodontidae from Australia and New Guinea*. Bureau of Mineral Resources Geology and Geophysics, Australia, Bulletin 85:149-160.
- Woodburne, M.O. 1967. The Alcoota Fauna, Central Australia: an integrated palaeontological and geological study. *Bureau of Mineral Resources, Geology and Geophysics, Australia, Bulletin* 87:1-187.
- Woodburne, M.O. 1969. A lower mandible of *Zygomaturus gilli* from the Sandringham Sands, Beaumaris, Victoria, Australia. *Memoirs of the National Museum of Victoria* 29:29-39.
- Woodburne, M.O., Tedford, R.H., Archer, M., Turnbull, W.D., Plane, M.D. and Lundelius, E.L. 1985. Biochronology of the continental mammal record of Australia and New Guinea. *Special Publication of the South Australian Department of Mines and Energy* 5:347-363.

Accepted 15 May 1992